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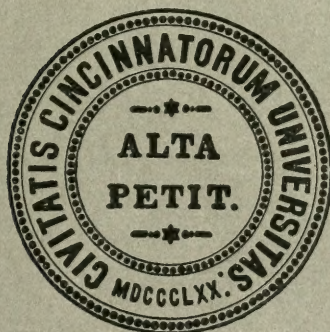
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Morphology of the Myxinoidei

By

Howard Ayers and C. M. Jackson



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Morphology of the Myxinoidei*

I. SKELETON AND MUSCULATURE

(CONTINUED)

C. REMARKS ON HOMOLOGIES

HOWARD AYERS AND C. M. JACKSON

1. Introduction

2. Cranium

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Mandibular Arch

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First and Second Branchial Arches

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4. Conclusion

*Contributions from the Morphological Laboratory of the University of Cincinnati

Ever since Müller described the anatomy of the head of *Bdellostoma*, comparative anatomists have constantly sought for the evidences of the relationship of the Marsipobranchii to the rest of the vertebrate stock.

We propose now to discuss the homologies of the head-skeleton of *Bdellostoma*—as a basis for the more general statement of the homologies between the Cyclostomes and Gnathostomes. Professor Huxley (1) announced several years ago that "There appears to be no sufficient foundation in the present state of knowledge for regarding the Marsipobranch skull as one which departs in any important respect from the general vertebrate type." A contrary view has more recently been published by Prof. Howes (2). We quote his statement in full for the reason that it represents the generally accepted view as to the position of the Marsipobranchii, as shown by a study of their morphology. He says, (p. 141) "In view of the admitted importance of that (referring to the relations of the pituitary body) it testifies, to my mind, to an enormity in the gap between the Marsipobranchii and the remaining Vertebrata which even Balfour's conclusion that the former are the "remnants of a primitive group" and Haeckel's famous aphorism that they are further removed from the fishes than the fishes are from man, insufficiently expresses. It disposes of the attempts to prove that "connecting links" between the Marsipobranchii and the higher Vertebrata are known to us; and it is, to me, a question as to whether it does not warrant a greater than a class distinction, viz : the subdivision of the sub-kingdom Vertebrata into two lesser sub-kingdoms ; the one *Epicraniata* for the reception of the Marsipobranchii alone, the other, *Hypocraniata* for all the higher forms." It is not necessary to quote from other authors since these two views represent fairly well the two groups of anatomists—the one of which has affirmed that there exists between the Marsipobranchii and remaining Vertebrata so close a relationship that a general homology

of the parts may be established, the other of which maintains that there is no relation between these two groups of animals save that of their common vertebrate ancestry. Naturally, in attempting to solve this problem recourse is first had to the anatomy of the head. No one had previously established clearly the homologies of the cephalic skeleton, though Huxley very suggestively carried through a comparison of the *Myxine* and *Petromyzon* skulls with those of the higher vertebrates. He did not, however, work out his views in final shape, nor does his work show that he even approached a correct solution of the problem. All anatomists, Huxley included, have accepted Johannes Müller's view concerning the nature of the structure peculiar to the *Marsipobranchii*, viz: the so-called "tongue." And all have apparently overlooked the fact that were this a tongue or tongue-like organ, it would be a great anomaly in vertebrate anatomy; since none of the fishes, even the higher fishes, possess a tongue or even a tongue-like organ. The homology of this organ with the vertebrate tongue has never been discussed, nor do we know of any efforts to determine the true nature of this organ. In our efforts to establish the homology of the parts between the *Marsipobranchii* and the *Gnathostomes*, we were at once confronted with the so-called tongue, and after a careful investigation of the whole subject, we find that by determining the nature of this organ, we have solved the puzzle of *Marsipobranch* head morphology. Dr. Ayers began this investigation at the Hopkins Seaside Laboratory in the spring of 1892, and continued at the University of Missouri during the years 1896-98, where Mr. Jackson joined him in the work.

The importance of the so-called tongue of the head in the solution of the morphology became apparent to Dr. Ayers in 1892 while he was studying the motions of the organ in the living animal, and he then discovered that it was not a tongue, but probably the transformed jaw apparatus. The careful study of the details of the anatomy of *Bdellostoma* which we here present, conclusively prove, we think, this to be a fact.

As we have shown in a preceding section (3) the cranium in *Bdellostoma* remains in an exceedingly primitive stage of development throughout the entire life of the animal. It proves conclusively by its anatomical characters, that it is strictly homologous with the embryonic cranium of the higher vertebrates.

All of the variations which appear in the higher forms during their progress to the adult condition are added to the simple cranium as represented in the adult form of *Bdellostoma*.* In regard to the visceral head skeleton, we find adhesions and separations which complicate the problem to a considerable degree, and some of which, so far as we know do not occur among the *Gnathostomata*.

The space enclosed by the trabeculae and hypophysial plate (the hypophysial fontanelle) is occupied in *Bdellostoma* by the hypophysial tube, which therefore apparently perforates the floor of the cranium. It is more correct, however, to consider that this relation is due to an extension forward of the trabeculae to surround the hypophysial sac, since the latter is phylogenetically and ontogenetically the older structure. In *Petromyzon* and the higher fishes there is no communication between the hypophysial sac and the mouth or pharynx, and the hypophysial fontanelle is relatively smaller. The hypophysial plate seems to represent a depressed portion of the cranial floor, and is probably in part homologous, with the basisphenoid of higher forms. Its continuity with the trabeculae was overlooked by Müller. The lateral bars which in a dorsal view (after the nasal tube has been removed, fig. 3) seem to continue the trabeculae forward, and are evidently *palatine* cartilages.

The nasal tube† in *Bdellostoma* continues forward in the median line of the cranial axis to the anterior end of the head. The relation observed in *Petromyzon*, where the nasal tube is small and opens dorsally a considerable distance behind the anterior end of the head, is secondary. It is due to the enormous growth of the cartilages (excluding nasal tube) concerned in the development of the *suctorial* apparatus of *Petromyzon*. The lateral plates of the olfactory capsules are the homologues of the *ethmoids* of higher forms.

* Even *Petromyzon* shows a slightly higher stage of development, since in that form the *sides* as well as the base of the cranium are cartilaginous, while in *Bdellostoma* only the *base* is cartilaginous, the remainder of the cranium being membranous. The Auditory capsules are also simpler in structure in *Bdellostoma* than in the *Petromyzontes*.

† The nasal tube of the *Cyclostomes* really represents nasal duct—hypophysial canal—since it forms a common exit for, and is formed by a common involution of, the nasal and hypophysial sacs.

Proceeding now to consider the *prepalatine* system of cartilages (Figs. 2, 3, including the subnasal, N, cornual, cc, labial TI, be, and tentacular cartilages 1, 2, 3, 4), we find that, although they present practically the same relations to the rest of the skull as in *Petromyzon*, their homologies have not hitherto been clearly recognized. For example, Johannes Müller (4) says: "Alles was daher bei *Petromyzon* vor dem Schädel und dem mit ihm verwachsenen harten Gaumen hat bei den Myxinoiden nichts ähnliches, und das sind der Lippenring, die zwei Seitenplatten, das vordere und das hintere Mundschild." A careful examination, however, reveals that each of these parts has a homologue in Myxinoids. Briefly stated, they are as follows:

<i>Petromyzon.</i>	<i>Bdellostoma.</i>
Annular Cartilage.	Labial and Tentacular Cartilages (in part).
Antero-lateral Cartilages.	4th Tentacular Cartilages.
Antero-dorsal Cartilage.	Subnasal Cartilage.
Postero-dorsal Cartilage.	Palatine Cartilages.
Postero-lateral Cartilages.	Cornual Cartilages.

This group of cartilages corresponds to the annular ring of *Amphioxus* and to the extremely variable group of labial cartilages in the higher forms.

According to previous authors, the jaw apparatus of the Marsipobranchii is entirely wanting or has suffered such regressive changes as to nearly obliterate it. A careful investigation of the skulls of *Bdellostoma*, *Myxine*, *Petromyzon* and *Ammocoetes*, however, discloses the fact that the *entire mandibular arch is present*, although the relations of the several parts have been much altered from the usual gnathostome condition. The skeleton of the so-called "tongue" of the Marsipobranchii, with its paired, bilaterally symmetrical dentigerous plates (Figs. I, Y, D) is in reality the *homologue of the lower jaw*, i. e., the Meckelian cartilages, of the usual gnathostome form. The huge club-shaped "tongue" muscle is made up of the muscles belonging to this arch. They have been, in *Bdellostoma*, entirely separated from their primitive attachment to the palato-quadrates, and have been translated to their present position in a manner which will be made clear in a subsequent paper. In *Petromyzon*, the original attachments are still closely retained. The dental plate of

Bdellostoma is homologous with the two pairs of "accessory lingual" dentigerous cartilages of *Petromyzon*.

The *upper portion* of the mandibular arch, i. e., the palato-quadrate portion, has been generally recognized by Huxley, Parker, Fürbringer and others. As in the typical gnathostome condition, it forms the subocular arch (Fig. 1, PQ), and extends cephalad and caudad. The anterior prolongation, P 1, forms the palatine bar, as already described, while the posterior forms a commissure connecting with the hyoid arch. Since the palato-quadrate is fused superiorly with the base of the cranium, the Marsipobranch skull belongs to Huxley's autostylic type. In *Petromyzon* the subocular arch bears a process which Parker (5) calls the antero-lateral process of the subocular arch, but which we consider to be strictly homologous with the quadrate of the higher forms. The same process, reduced in size, is found in *Bdellostoma forsteri*, and occasionally in *Bdellostoma dombeyi*.

The free end of this process probably marks the point of primitive articulation of the (now detached) Meckelian cartilages.

The muscles of the "tongue" are innervated by fibus from the tregeminus nerve—a fact recognized long ago by Müller and more recently by Fürbringer (6). This fact alone ought to demonstrate the absurdity of attempting to homologize the structure in question with a tongue. On the other hand, it clearly indicates its true nature as a mandibular apparatus.

The cause which led to the separation of the Meckelian cartilages (dental plate) from the palato-ptyerygo-quadrate portion of the arch was doubtless the acquisition of the "rasping" habit in feeding, especially in situations which prevented the free motion of the jaw in the dorso-ventral direction, (as, for example, when burrowing *into* a carcass). With the development of motion of the lower jaw in the fore-and-aft direction, the connection of the Meckelian cartilages (dental plate) with the quadrate was loosened, and finally entirely separated. The separation of the Meckelian cartilages, and especially of the muscles from their original connection with the palato-quadrate has taken place to a much greater extent in *Bdellostoma* than in *Petromyzon*. In the latter, the muscle still retains in part its original attachment. Modifications and migrations of the mandibular arch are not uncommon among the lower Vertebrata. In many forms (e. g. *Scyllium*) the entire arch is loosely connected

with the cranium by ligaments. In the sturgeon the arch has lost all direct connection with the cranium, except through the hyo-mandibular bars. A striking illustration of transformation is seen in the formation of the *malleus* and *incus*, which are cut off from the proximal end of Meckel's cartilage, removed from their original location, and enclosed in a special chamber where they serve an entirely new function. With these examples in mind we can readily comprehend the state of affairs just described in the Marsipobranchii, where, notwithstanding their transposition, the parts still subserve their original function.

Immediately behind the palato-quadrate cartilage, a second bar extends from the auditory capsule, as previously described. (Figs. 1, 2, 3, Hy). This is the upper portion of the hyoid arch. In Myxinoids, this arch is connected to the palato-quadrate by two processes; in *Petromyzon* (Fig. 6) by only one. The ventral portion of the hyoid arch, like the mandibular, has become detached from its primitive position. The basal portion of the hyoid arch in *Bdellostoma* forms the anterior segment of the basal plate. In *Petromyzon*, it is apparently represented by the "median ventral cartilage" of Parker.

The basal plate (Figs. 5 and 1) of *Bdellostoma* is a structure almost as interesting as the "tongue" itself (for which it forms a support). As previously described by us, it is made up of three segments. Of these, the posterior (B'') is composed, not of true cartilage, but of a chondroidal tissue, and is certainly not to be considered as homologous with any part of the visceral arches. It is merely a condensation of the tendinous tissue in the median ventral raphe of the *constrictor musculi mandibuli*. The anterior segment (B) of the basal plate evidently represents the *basi hyoids* and copulae. The middle segment (B') as shown by its connection with the two branchial bars (Fig. 1, br., br.2) is probably similarly formed by a fusion of the ventral portion of the first and second branchial arches (third and fourth *visceral* arches.)

In *Petromyzon*, the middle segment of the basal plate is wanting. The large "lingual cartilage" is equivalent to the posterior segment in *Bdellostoma*, and the "median ventral cartilage" to the anterior segment.

As to the visceral skeleton behind the hyoid arch, we have already pointed out that the two prominent lateral cartilagenous

strips (Figs. 2, 3, 5, br. 1, br. 2) represent the 3d and 4th visceral arches (1st and 2d branchial bars) whose ventral portions have fused together to form the middle segment of the basal plate.

It is also altogether probable that the complicated velar framework of cartilages (Figs. 1 and 3, V, V', ab, pb, etc.) represent the skeleton of a set of metamorphosed branchial arches. In this connection it is important to remember that, as Price (7) has shown, several of the most anterior branchial clefts *appear transiently* in the embryo, and soon disappear. It is to these branchial clefts that the metamorphosed branchial arches found in *Bdellostoma* evidently belong. The degeneration of the anterior branchial sacs is undoubtedly due to the enormous growth of the club-shaped "tongue" muscle, which in pushing backward necessarily encroaches upon the branchial territory. As the club-shaped muscle is much less developed in *Petromyzon*, the latter form has not undergone so much modification in the anterior branchial region.

In the posterior branchial region we find a set of cartilages, now described for the first time, which represent the *branchial arches* (V. preceding section of this paper). They are comparatively small in size, but lie imbedded in the walls of the external branchial passages (i. e. gill clefts), and undoubtedly are the representatives of the complicated "branchial basket" found in *Petromyzon* (fig. 6). The relation becomes evident when we examine the skeleton of a young *Petromyzon* embryo (fig. 7). The figure shows that at an early stage the branchial basket of *P.* appears as a series of slender bars, each partially enclosing the corresponding gill slit, and connected only by a ventral connecting strip. With the exception of the latter the relations are identical with those found in adult *Bdellostoma*. It is also important to note that the gill bar corresponding to the oesophagocutaneous duct (which is really a modified gill slit) extends along the duct *to the wall of the pharynx*, upon which it often expands to a greater or less degree. It is evident, therefore, that no distinction between the Cyclostome branchial cartilages (as "*extra branchials*") and those of the remaining vertebrates can properly be drawn.

Our most important conclusions concerning homologies of the Myxinoid skeleton may be summarized as follows:

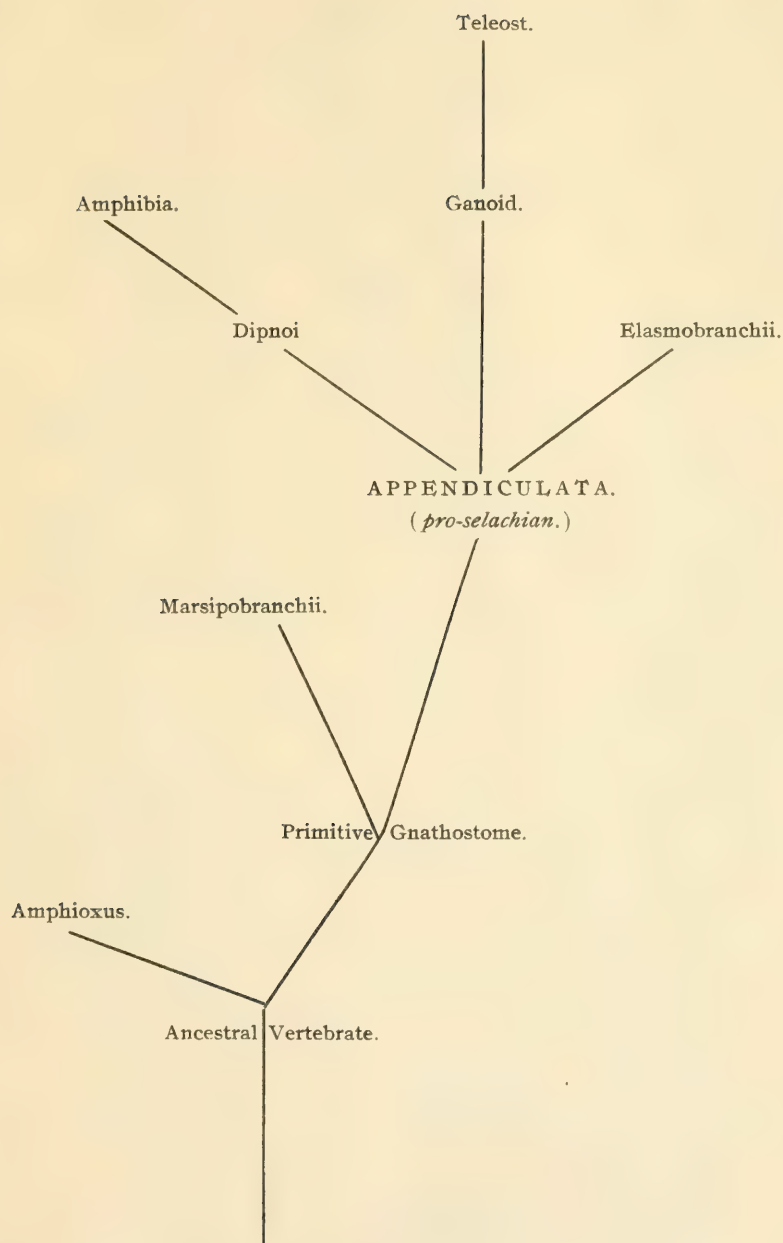
1. The discovery of the series of rudimentary gill bars in

Bdellostoma, and the true interpretation of the circumoral and 'lingual' regions in Bdellostoma and Petromyzon enables us to establish completely the homologies within the Marsipobranch class.

2. The discovery that the so-called "tongue" of the Marsipobranchii is in reality the detached lower jaw solves the puzzle of Myxinoid morphology, and makes clear their general relation to the remaining vertebrates. They are *true Gnathostomes*, forming a primitive group which probably sprang from the common ancestry before the acquisition of paired appendages by the vertebrate type. The relation of the Marsipobranchii to the vertebrate stock is shown in the diagram on the opposite page.

REFERENCES:

- (1) Huxley, T. H. Cranio-facial Apparatus of Petromyzon, Journal of Anat. & Physiol., Vol. X. p. 427.
- (2) Howes, G. B. Transactions of the Liverpool Biological Society, Vol. VI.
- (3) Ayers, Howard and Jackson, C. M. Journal of Morphology, XVII. No. 2.
- (4) Müller, Johannes. Anatomie des Myxinoiden.
- (5) Parker, T. J. Zootomy, p. 3.
- (6) Fürbringer, P. Muskulatur des Kopfskelets Jen. Z. N. F. II.
- (7) Price, G. C. Some Points in the Development of a Myxinoid. Verh. der Anat. Gesellschaft, X. '81.



EXPLANATION OF FIGURES 1, 2, 3, 4, PLATE I.
AND FIG. 5, PLATE II.

- A, auditory capsule.
a, anterior connecting process.
Ae, external bars of anterior segment.
Ai, internal bars of anterior segment.
ab, anterior transverse velar bar.
B, anterior segment of basal plate.
B', middle segment of basal plate.
B'' posterior segment of basal plate.
br., br., 1st and 2d branchial arches.
cm, palatine commissure.
Cr, cranium.
cc, cornual cartilages.
D, dental plate.
Hy, hyoid arch.
H.p., hypophysial plate.
L.c., lateral labial cartilage.
Nt, notochord.
O.C., olfactory capsule.
p.b., posterior transverse velar bar.
Pl., palatine bar.
P.Q., pterygo-quadrate.
t, tendon of retractor mandibuli.
Tr, trabecula.
T.I., transverse labial cartilage.
V, V', external and internal lateral velar bars.

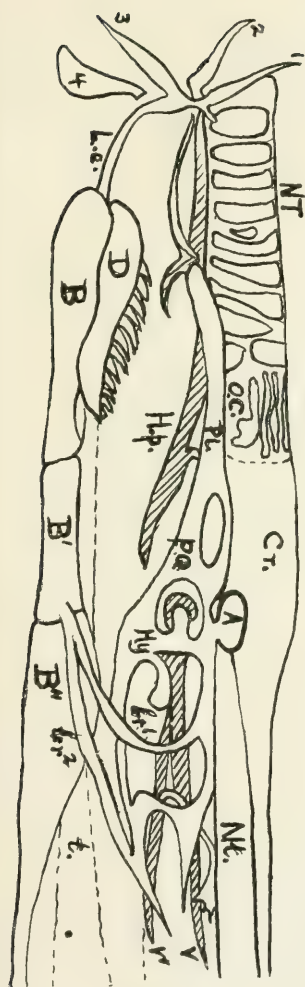


Fig. 1.

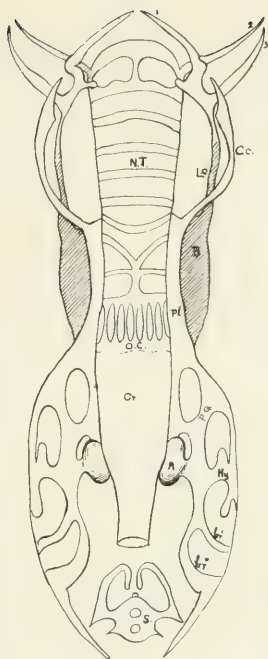


Fig. 2.

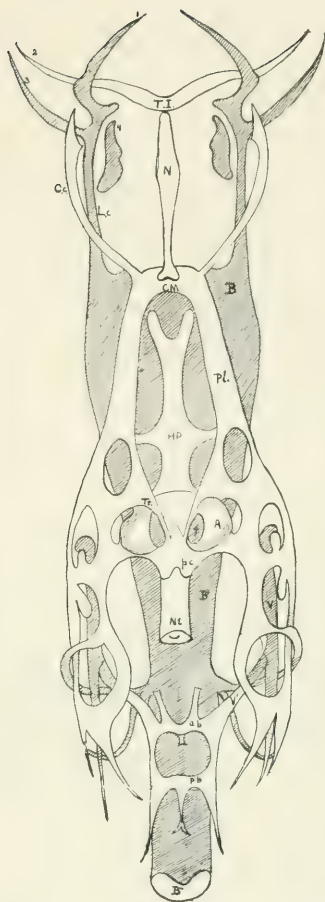


Fig. 3.

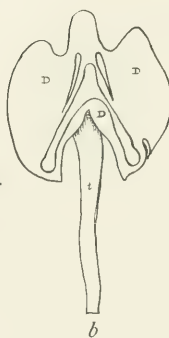
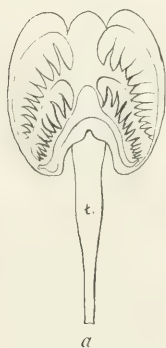


Fig. 4.

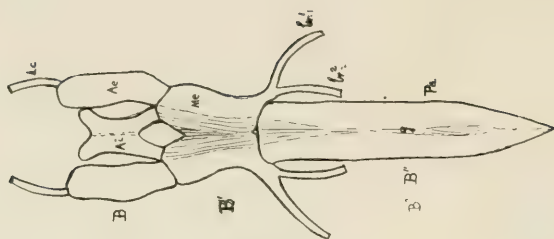


Fig. 5.

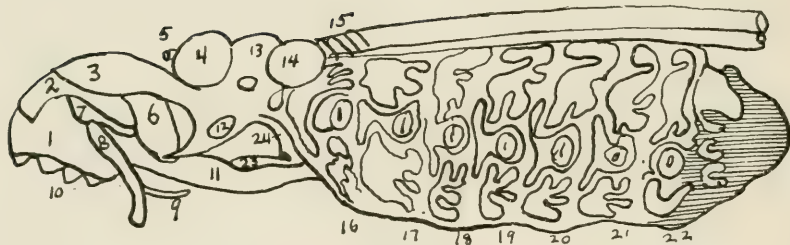


Fig. 6.

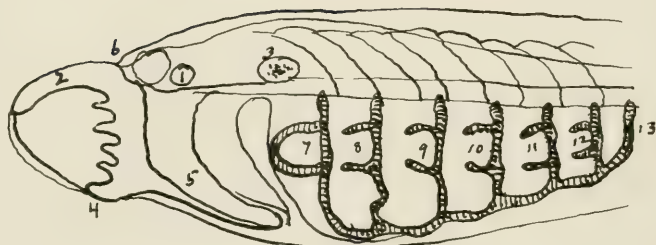


Fig. 7.

EXPLANATION OF FIGURE 6, PLATE II.

ADULT PETROMYZON SKULL (lateral views).

Homologous with Bdellostoma.

1. Annular ring ("Lippenring")Labial and tentacular cartilages.
2. Antero-dorsal Cartilage.....Sub-nasal cartilage.
3. Postero-dorsal " Palatine cartilage.
4. Nasal capsuleOlfactory capsule.
5. Nasal tubeNasal tube.
6. Postero-lateral cartilagesCornual cartilages.
7. Antero-lateral cartilagesFourth tentacular cartilages.
8. Styliform cartilages.....Tentacular cartilages.
9. Medium ventral cartilageAnterior segment of basal plate.
10. Labial teeth.....Labial teeth.
11. Lingual cartilage.....Third segment of basal plate.
12. Sub-ocular archSub-ocular arch.
13. CraniumCranium.
14. Auditory capsuleAuditory capsule.
15. Neural archesNeural arches where present.
- 16-22. Branchial bars.....Branchial bars.
23. "Cornual" cartilageHyoid arch.
24. Styloid process.....Hyoid arch.

EXPLANATION OF FIGURE 7, PLATE II.

EARLY EMBRYO OF PETROMYZON (after Schulze).

- 1, eye.
- 3, auditory capsule.
- 2, 4, annular cartilage.
- 5, styliform cartilage.
- 6, Nasal capsule.
- 7-13, branchial bars.

